The Origin of the African Flora

An Inaugural Lecture

GIVEN IN THE UNIVERSITY COLLEGE OF RHODESIA AND NYASALAND

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INTRODUCTION

I HAVE chosen as the subject of this Inaugural Address the question of the Origin of the African Flora, a fundamental problem which appears especially appropriate for study here in the youngest college of this ancient continent. During the course of this evening I shall endeavour to describe not only why the Federation may be considered to be located geographically in one of the most favourable centres for the study of this continental problem, but also how it is so situated as perhaps one day to make an essential contribution towards the satisfactory solution of the greater problem of the origin of the modern vegetation of this earth.

As with all scientific investigations, the study of the Origin of the African Flora requires first an examination of the terms and difficulties which beset the subject, before the real problems emerge. The most obvious obtrusion is that the continent of Africa contains not one but several floras, and perhaps the final word in the title of this address should have been pluralized. There are, however, more complex questions than this to be resolved.

In botanical terminology it is usual to distinguish between a *flora* and a *vegetation*. A flora may be defined as the assemblage of recognizable taxonomic units, or *taxa*, which exists in any particular botanically distinct area; it is distinguishable from that of any other such area. The vegetation is the plant cover which results from the association of individuals of the various taxa of a flora into one

or more plant communities. A flora is studied primarily by taxonomists, while the vegetation is studied especially by ecologists. The nature of the vegetation of any particular area is determined by the selective interaction between individuals of various taxa of the flora and the environment, and by competition between the individuals themselves, but there is also a vital *historical* element which affects the availability in that area of particular taxa. A familiar temperate example of this is the absence of spruce from natural coniferous woodland in Britain; this particular species disappeared from that area during the Pleistocene Ice Age, but survived on the European mainland, where it remains an important element of coniferous woodland. Biogeographical studies must take into account not only floras and vegetation, but also this historical element and the factors from which it results.

Tropical Africa has no such immediately obvious internal barriers to plant migration as the seas or mountains of Europe, nor were the effects of the Pleistocene Ice Age apparently so devastating to the survival of species as in Europe. Around the coasts of Africa, however, lie various islands, which form an important exception to this rule. Isolated from the continental mass at different times, they now support what may be assumed to be relict floras from various past epochs. The correct interpretation of the present composition of these island floras will provide milestones in the progress of the plant colonization of Africa.

The flora of the African mainland has been subdivided by different workers into a varying number of floral regions. An early scheme still in wide general use is that of Engler (1910), which recognizes some five subdivisions. One of the latest, which contains a number of additional regions, has been prepared by Good (1953). Even with

these additional regions however Good's scheme is, as far as Africa goes, an incomplete statement of broad floral relationships. Reference to papers on the distribution of African plants such as a recent work by Milne-Redhead (1954) will show that there is often a distinct overlapping of the examples he selects over several of Good's regions. Moreover the scheme fails to show the close relationships between the flora of the Lowland Rain Forest of East and West Africa, between the Upland Savanna of East, West, and Central Africa or between the Upland Forest of these latter regions and Ethiopia.

It might be maintained that the extent to which Good's scheme does to some extent reflect floral relationships is due to vegetational resemblances, from which arise, in so far as certain of them are ignored, the main criticisms. Some workers have indeed questioned whether a floral region can be mapped, and Cain (1947) prefers to use the concept of a *Natural Area.* This is a more comprehensive and generalized unit determined by the environmental, floristic, and historical features of particular vegetation. A number of Belgian and French workers in Africa have in fact employed such a unit in the preparation of chorological maps, although not necessarily referring to it by this name. As biogeographical studies have to be based on some classificatory unit, large or small, there are some advantages in starting from broad *Vegetation Types.*

It is unfortunately by no means easy to classify the vegetation of Africa into a limited number of vegetation types, although the difficulties can to some extent be reduced by over-simplification of the complexity of the vegetation. When this is done it would appear that these simplified basic vegetation types represent distinct floristic groups and that their distribution may indeed be taken to indicate the

extent of distinct floral regions. What is mapped in this way is in fact the primary natural areas of Africa. From this basis it is possible to proceed to a consideration of the origin of the flora of each of the regions.

The present considerations have been entirely restricted to a study of the dominant plant type of the modern world, the Flowering Plants, and because of limitations of time refer only to that area of Africa which is south of the Sahara.

THE VEGETATION TYPES OF AFRICA

The first basic subdivision of African vegetation is into *forest* and *savanna*. In forest the tree canopy is sufficiently dense to exclude all but a small group of specialized grasses; the canopy persists throughout the year, the vegetation never burns. In savanna the tree canopy is light enough to permit the growth of grasses, which results in annual grass fires, except where these are specially controlled; trees, when present, are deciduous in the dry season and in order to survive must be fire-resistant.

Both forest and savanna appear to change in structure and composition above an altitude of about 2,500 ft. The tree line in Tropical Africa lies around 9,000 ft., so that the two forest types, *Lowland Forest* and *Mountain Forest*, can be defined altitudinally. Above about 9,000 ft. and up to approximately 15,000 ft. special and very interesting plant communities occur which can here be classified simply as *Mountain Communities*. *Lowland Savanna* and *Upland Savanna* may be similarly altitudinally divided, changing at approximately 2,500 ft., and merging at some higher point into Mountain Communities. The greater part of South Africa lies outside the tropics and its pre-

dominantly 'veld' vegetation can be grouped as *South African Temperate*. The extreme south of the Union is covered by the very interesting '*Cape Flora*'.

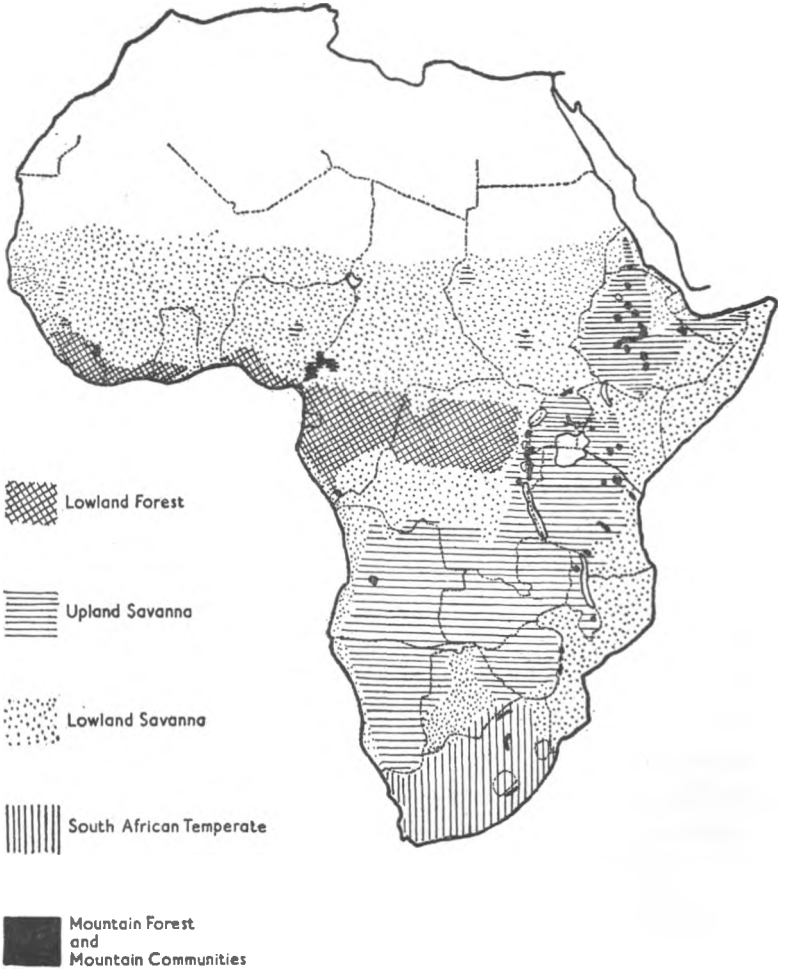

FIG. 1. Distribution of primary Natural Areas in Africa south of the Sahara; these are taken to indicate major floral units

A map of Tropical and Southern Africa with the vegetation plotted into these main subdivisions is shown in Fig. 1. Reference again to works such as those of Milne-Redhead (1954) shows that the distribution range of many specific taxa can be fitted into one or other of these major ecological divisions. Such a correlation supports the suggestion that the distribution of these basic and often discontinuous vegetation types coincides with that of major and correspondingly discontinuous floral regions. If it can be assumed that the distribution of these vegetation types does represent in this sense the extent of the various primary natural areas and so of the major floral regions, it is possible to proceed to a consideration of the origin of the several floras. First, however, some reference must be made to the more fundamental problem of the origin of flowering plants themselves.

PRIMITIVE FLOWERING PLANTS

There has been plant life on the land for at least three or four hundred million years, as the occurrence of fossils in Devonian rocks bears witness. The flowering plants, which today dominate the vegetation of all major areas of the earth's surface, are unknown as fossils before Jurassic times. Their presence is not universally regarded as demonstrated conclusively, and they do not occur in any significant numbers, before the Cretaceous. While this circumstance was once widely interpreted as indicating that flowering plants arose during the Jurassic or Cretaceous periods, a number of palaeontologists have now considered this assumption unwarranted. Thus Seward (1931) stated,

> . . . these oldest known samples of petrified wood confirm the conclusion, based on the still older leaves of the Arctic plane

trees, that the oldest dicotyledons which clearly reveal their kinship with Flowering Plants are old only in a geological sense and astonishingly modern in their anatomical features. They confirm our belief in an antiquity of angiosperms antedating by many millions of years, probably by several geological periods, the first appearance of recognizable pioneers of the present ruling dynasty in the modern world.

Campbell (1943), after a review of the fossil evidence, concludes that flowering plants must have existed earlier in the Mesozoic era, and have become well diffused before the Eocene period.

One difficulty in searching for early angiospermous fossils, as has been remarked by Hamshaw–Thomas (1936), is that there is no clear picture of what one is looking for. A very interesting objective approach to the solution of this problem is suggested by the work of Sporne (1949), who examined statistically the frequency and distribution of a range of characters in flowering plants considered as 'primitive' and 'advanced'.

A more subjective approach is that of Hutchinson (1928, 1934, 1948), who has prepared a classification of the families of flowering plants based upon his assessment of their interrelationships. While Hutchinson's scheme can be criticized on various points and is by no means universally accepted, it is considered by many botanists to constitute at least the best such phylogenetic scheme so far advanced. Briefly, Hutchinson suggests that modern flowering plants fall into two groups, the Herbaceae, fundamentally and predominantly herbaceous, and the Lignosae, fundamentally and predominantly woody. The Herbaceae evolved from plants with many of the characters of the modern Ranunculaceae, the Lignosae from ancestors resembling in many ways the modern Magnoliaceae. Hutchinson does not speculate as to

whether these two groups arose from a common ancestral flowering plant group, or whether they evolved separately.

As to where we may search for evidence of the real existence of such hypothetical ancestral groups, there is at present little clear indication. It is, however, possible to make a number of theoretical deductions. In the biological world it is unusual for fundamental organs to be evolved more than once, and in totally unrelated groups. The search for ancestral flowering plants may therefore commence with a study of the Pteridosperms, the most ancient fossil group possessing a unique and essential character in common with flowering plants, the *seed*.

The Pteridosperms were a group of fern-like shrubs or small trees, reproducing by means of structures which have been recognized as essentially similar to the seeds of flowering plants. They reached their zenith during the Late Carboniferous, when they formed both numerically and structurally the largest group in the contemporary vegetation. The Pteridosperms grew in a swampy open woodland type of vegetation associated earlier or later with true Ferns, Conifers, Cycads, Equisetales and certain extinct plant forms. Most of the groups in this woodland have at one time or another been considered as the possible ancestors of the flowering plants, for two of them and several other infrequent contemporary forms also reproduced by seed-like structures.

Before pursuing this question further it is necessary to examine what is known of the land surface of the earth during the Late Carboniferous and Early Permian times in which the Pteridosperms flourished.

EARLY CONTINENTS

That the present distribution of continents and oceans over the surface of the earth has not persisted from the

beginning of geological time has long been propounded. The most confident statement of the origin and development of the present continental masses was presented by Wegener (1923), and later modified and amplified by du Toit (1937). According to Wegener's hypothesis, as amended by du Toit, there were during the Carboniferous epoch two main continental masses, one in the Northern Hemisphere (Laurasia) and one (Gondwanaland) in the south (Fig. 2). Both these continental masses were even-

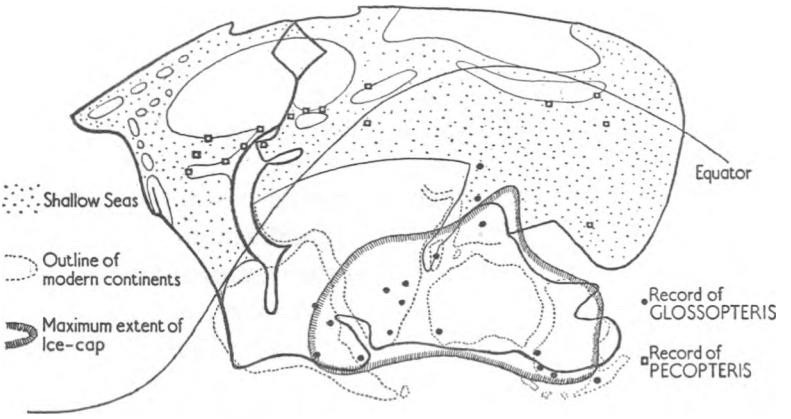

FIG. 2. Distribution of continental masses during the Late Carboniferous Period, after Wegener and du Toit; the probable position of the contemporary southern polar Ice-cap, and of the *Pecopteris* and *Glossopteris* floras are also indicated

tually split by Continental Drift, the fragments of Gondwanaland beginning to drift far apart in the Early Cretaceous, although probably not finally separating until the Eocene. Wegener and his supporters marshal evidence from many sources in support of this theory; he himself further postulated (Koppen and Wegener, 1924), in addition, a shifting of the position of the climatic poles on the earth by disturbances to its axis of rotation.

There has recently appeared (Runcorn, 1955) some rather surprising confirmation of pole-wandering from the evidence of the permanent magnetization of rocks, but some workers regard this as support for a mutually exclusive alternative theory to that of Continental Drift.

Of Wegener's theory du Toit (1954) writes:

> The extraordinary, though well-established similarities and analogies displayed by those several lands (of the S. Hemisphere) in respect of their stratigraphies, orogenies, volcanisms, past climates, faunas, floras, and physiographies thereupon become more clearly and logically explicable than under the orthodox view that the parting oceans originated through the subsidence of huge sections of a far greater parent continent.

On the other hand many geophysicists do not accept Wegener's hypothesis or later modifications of it. The principal objections are based on the improbability of any continental sliding movement (Umbgrove, 1951) and the absence of any force sufficient to produce it (Jeffreys, 1951). Jeffreys issued a plea for objectivity: '. . . at present all accounts of the relevant facts are under suspicion of selection to fit a particular opinion, and I think that the time has come when a general account of the facts of past distributions of fauna and flora should be produced without regard to a particular theory'. This is indeed a worthy aim, but when two opposing geological views are widely held, the biologist, who is ill equipped to weigh the merits of geophysical evidence, may be excused for selecting and using the theory which greatly simplifies the task of rationalizing distribution phenomena.

One further relevant advantage of Wegener's theory is that it offers an explanation for the anomalous Permo-Carboniferous glaciation, which, as will be explained, must

have had an even more momentous effect on plant distribution and evolution than the succeeding Pleistocene glaciation.

There have been, it is thought, some four major glacial periods in the known history of the earth, occurring at intervals of approximately 250 million years, and associated with periods of mountain building (Brooks, 1926). Geological evidence suggests that during the third of these, the Permo-Carboniferous glacial period, the Southern Ice-cap extended over the area indicated in Fig. 2. There is no trace of the Northern Ice-cap, other than the presence of tillites (boulder clays) in Alaska, and it is therefore believed to have formed largely over the sea.

By assuming the correctness of Wegener's deductions as to the distribution of the continents and the polar ice-caps during the Late Carboniferous and Early Permian, it is possible to obtain a fair picture of the distribution of the contemporary vegetation in which flowering plants may have evolved.

POSSIBLE MODE OF ORIGIN OF FLOWERING PLANTS

The Pteridosperm vegetation at the time of the Permo-Carboniferous Glacial Period was not uniform, but divided into tropical and temperate floras. The warmer areas were dominated by forms referred to the genus *Pecopteris*, the cooler by the genus *Glossopteris*. The distribution of the two floras relative to the Wegener reconstructions is shown in Fig. 2.

The modern flowering plant families usually adjudged as possessing the largest number of primitive features, the Ranunculaceae and Magnoliaceae (*sensu latuo*), are essentially temperate groups. It seems probable from this that their ancestral forms were also temperate, for many of such

modern families that are restricted as to temperature range are fairly consistently either temperate or tropical. If flowering plants evolved from Pteridosperms, it is most likely therefore that they arose from some element of the *Temperate Glossopteris* flora of Gondwanaland.

The Permo-Carboniferous Glacial period, as in the case of the later Pleistocene Ice Age, was not continuously cold. The records of fossil distribution show that the *Glossopteris* flora grew at times close to the Southern Ice-cap. During the other extreme, at the glacial maxima, vast areas of *Glossopteris* woodland would be destroyed by the extension of the Ice-cap. Large areas of land suitable for plant colonization would accordingly be exposed by the periodical melting of the Ice-cap, and in these virgin habitats new plant forms would have the greatest opportunity for successful establishment. The ancestral flowering plants may well have appeared during this period on such a terrain.

Assuming for the moment that this mode of origin were possible, it can be postulated that at some time during the Late Carboniferous or Early Permian a group of flowering plants, resembling in many ways the modern Ranunculaceae, was established on the continent of Gondwanaland, near what has now become the coast of Southern Africa. Some thousands of miles away, near what is now the south-west coast of modern India, a second group arose, similar in many respects to the modern Magnoliaceae. Most probably these two groups evolved separately from some proto-angiospermous ancestor, perhaps a widespread type still classified as a Pteridosperm. The reasons for postulating the appearance of the two ancestral angiospermous groups in these particular areas of Gondwanaland will be considered later.

There is considerable evidence suggesting the indepen-

dent origin of two groups of early Angiosperms. While both may at first have been composed of woody, and largely phanerophytic forms, for they had to survive competition in a woodland environment, only one group remained predominantly so. The ranunculoid forms gave rise to the modern groups which Hutchinson classifies as Herbaceae, and quite early a great range of herbaceous types must have differentiated. The magnolioid forms by comparison produced mostly woody forms, evolving to form the modern Lignosae.

The absence of modern groups intermediate in character between Herbaceae and Lignosae suggests that not only did these groups have a separate origin, but also that this was geographically distinct. Hybridization between some members of these two early groups would have been virtually unavoidable had they been closely related in both time and space. When their derivatives did eventually meet, genetical differentiation must have proceeded so far as effectively to prevent inter-breeding.

By the close of the Permo-Carboniferous Glacial Period, it can be supposed that differentiating forms of Herbaceae and Lignosae were established in these two regions in the *Glossopteris* woodland and along its fringes, and were beginning to spread.

Du Toit (1937) gives a vivid picture of the geological period following the final retreat of the Permo-Carboniferous Ice.

> The Permian saw the development over the very region previously ice-capped—including in this the eastern side at least of Antarctica—of vast lakes, swamps and forests, and of coal forming from the *Glossopteris* vegetation, more particularly at two periods. That the climate was not only wet but cold, at least in many places, can be deduced from the inferred proximity

to the pole, the presence of local ice in Australia, the limited development of fire-clays beneath the coal-seams, the presence of fossil wood showing annual rings and the abundance of undecomposed felspars in the associated sandstones. . . .

By the end of the Permian, the Herbaceae may have spread over the whole of that portion of Gondwanaland now remaining as South America, Southern Africa, India, Madagascar, and a part of Antarctica. Although represented by some woody forms, it is possible that the Herbaceae as a group were unable to spread successfully through the *Glossopteris* woodland. Increasing numbers of herbaceous forms would instead colonize the fringes of the woodland and other habitats unfavourable to *Glossopteris* and its associates. To the south such habitats would be colder, while to the north they probably extended higher altitudinally and again would therefore be cooler. The Herbaceae remained accordingly predominantly temperate forms.

The Lignosae on the other hand, being phanerophytes, could establish themselves in and spread through the *Glossopteris* woodland. Starting from temperate magnolioid forms established on areas uncovered by the retreating ice, the differentiating groups of Lignosae would produce not only forms adapted to the more temperate *Glossopteris* woodland, but also others capable of establishment on suitable warmer areas to the north of it.

It is very probable that during the Permian, elements of both the Herbaceae and Lignosae crossed the Tethys Sea and became established in the Northern Hemisphere. The Tethys cannot have been a complete barrier to intercontinental migration, and probably the sea was temporarily bridged at various geological intervals. Du Toit (1937) expresses the opinion that the current conception of the Permo-Triassic Tethys as a regular trough of more

or less uniform width and depth is erroneous, the evidence pointing towards land-bridges across it, e.g. in Persia.

There is an apparent contradiction in the assumption that groups of Herbaceae adapted to cold, and groups of Lignosae adapted to warmer conditions would contemporaneously cross the Tethys. Such crossings could clearly have been made only at different altitudes and in different areas or at different times. It is to be noted in this respect that the tropical *Pecopteris* and temperate *Glossopteris* are believed by some workers to have equally succeeded in this continental transmigration during the Permian.

It seems extremely probable that the Hercynian orogenies which preceded the Permo-Carboniferous Glaciation had left high plateaux over Gondwanaland and Laurasia, not as yet greatly eroded by peneplanation. One estimate postulates a contemporary Gondwanaland plateau over what is now Africa at approximately 12,000 ft. The Herbaceae could colonize such plateaux and the Lignosae the lowland coastal areas. Neither group as yet would contain sufficient individuals to be detected in the fossil floras investigated by present techniques.

More particularly among the forms which crossed the Tethys, but also in Gondwanaland, increasing geographical isolation must already have resulted in the formation of many genetic groups resembling those such as are represented by modern Caryophyllaceae or Geraniaceae. Indeed differentiation must have proceeded to the species level in some instances before the trans-Tethys migration, as will be discussed later.

DEVELOPMENT AND SPREAD OF EARLY FLOWERING PLANTS

The next epoch, the Triassic, was warm and dry. It was also very long, four times as long as the Permian. Deserts

were extensive, and in virgin habitats around their margins where rainfall was intermittent and sporadic, the new flowering plant groups, especially the Herbaceae, would perhaps be able to survive or establish themselves much more readily than their Pteridosperm competitors. Indeed during the Upper Permian and Triassic periods the Pteridosperms suffered a steady decline, Conifers, Ferns, and Cycadophytes becoming relatively more important. There are still no clear fossil indications of the presence of flowering plants, although some leaves named *Furcula granulifera* from the late Triassic of Greenland might be angiospermous.

The Lignosae, during the Permian trans-Tethys migration, would have split off tropical groups such as are now represented by Rosaceae, Tiliaceae, and Hammamelidaceae. The tree groups would not spread so extensively away from the restricted areas of Triassic woodland, although many of the early groups, now differentiating under tropical conditions, evolved northern or southern temperate forms on the colder limits of their distribution. Some of these, especially groups near to and perhaps derived from the Hammamelidaceae and Ulmaceae, such as Betulaceae (*sensu latuo*) and Platanaceae, appear to have spread over the Northern Hemisphere at the same rate as the Herbaceae.

On the periphery of Polar Gondwanaland, the Herbaceae had by the close of the Permian spread over what is now the modern South America, South Africa, Antarctica, and Australasia. Early on in this epoch there had been a major differentiation in the Herbaceae splitting off the progenitors of the Monocotyledons, and before the close of the Triassic the ancestral groups of the modern cosmopolitan families such as Polygonaceae, Gentianaceae, and Boraginaceae had been formed.

North of the Equator, the elements of those groups of

Herbaceae which had migrated across the Tethys Sea during the Permian also segregated as they spread in the Triassic, giving rise to the groups from which evolved the modern and entirely north temperate families such as the Adoxaceae, Resedaceae, and Fumariaceae.

During the succeeding epoch, the Jurassic, conditions were still warm, although perhaps not so dry. Most of the Carboniferous mountain masses had been eroded down, and the two main continental masses, still separated by the Tethys Sea, lay at a low elevation. Further migration of temperate forms across the Equator, which during the two preceding epochs could have taken a high altitude route, would now be impossible. Flowering plant migration during the Jurassic would have been restricted to movement within the individual continental masses, and probably at this time the temperate elements of Gondwanaland became continuous right round the then South Pole.

Unlike the original Herbaceae, their monocotyledonous offshoots had appeared under the tropical conditions of the later Permian, and were at first essentially tropical forms. In the Jurassic these early tropical groups of Monocotyledons differentiated to give rise to the ancestral groups of the modern families such as Liliaceae, Commelinaceae, and Palmae, spreading over the areas occupied by what is now the eastern coast of Africa and western coast of India.

Probably the Monocotyledons were polyphyletic in origin, for while the main group appears to have had a tropical origin in this manner and to resemble fairly closely the Helleboreae section of the modern Ranunculaceae, a second smaller group is mainly temperate and aquatic, resembling more the Ranunculoideae section. The limited distribution of both these groups of Monocotyledons in Australasia suggests that they originated much later than

the other cosmopolitan groups of Herbaceae and Lignosae, and had insufficient time to migrate to Australasia before it was isolated from the mainland of Gondwanaland.

Many authorities are prepared to admit the possibility of the occurrence of flowering plants during the Jurassic. Turrill (1948) says: 'It is very probable that true Flowering Plants existed in Jurassic times . . . in localities and under habitat conditions such that their remains could not be fossilized, for example, on mountains away from swamps and the sea coast.' Pollen of types suggesting the families Magnoliaceae, Nymphaceae, and possibly Juglandaceae, and wood resembling that of Winteraceae and Magnoliaceae, has been reported as present in deposits estimated as of Jurassic Age.

There is no doubt as to the presence of flowering plants in the next epoch, the Cretaceous, when they became the dominant fossil form, and must have existed over all the major temperate and tropical areas of the earth's surface.

On Koppen and Wegener's hypothesis, whose validity must for present purposes be assumed, the southern limits of the Northern Continent during the Cretaceous still lay astride the Equator. Much of what is now the Northern Hemisphere lay in the tropics, and the area which is now modern Greenland was so placed that it enjoyed a mild climate. Antarctica on the other hand lay centred over the South Pole; and the southern portions of Gondwanaland, now the southern extremities of South America, Africa, and Australia, together with New Zealand, lay close to the Southern Ice-cap. Probably at this time a special Antarctic flora evolved, with the break-up of Gondwanaland to remain as isolated relicts in the southernmost regions of these modern areas.

Du Toit (1937) maintains that, starting in the Jurassic,

and continuing through the Cretaceous, the continent of Gondwanaland had begun to fragment, and the individual portions to drift apart. This fragmentation actually occurred in both ancient continents, but was earlier and more complete in Gondwanaland. He suggests that during the Early Cretaceous, fragmentation had already proceeded so

FIG. 3. Distribution of continental masses in the Southern Hemisphere during the Early Cretaceous, after Wegener and du Toit

far that South America and Africa were joined only by their common southern extremity to an Antarctic continent, from which India and Australasia were also separating (Fig. 3). New Zealand is generally considered to have been isolated in the Cretaceous. Indeed, owing to a great marine transgression which occurred during the Late Cretaceous, all the individual portions of Gondwanaland must have been completely, but not permanently, separated at that time.

Du Toit (1937) postulates that in the Late Cretaceous

regression, and during the Early Eocene period of the Tertiary epoch, South America was again connected to Africa, from near the Amazon region to the West African bulge, and to Australasia via the Antarctic. India was isolated. The Northern Continent, though still continuous, was connected only via the Behring Strait.

During the Eocene, Oligocene, Miocene, and Pliocene periods of the Tertiary epoch, the climate continued dry, and possibly from towards the close of the Oligocene became also cooler. Gondwanaland continued to fragment, and after the close of the Eocene, South America appears to have become detached from Antarctica to the south, while probably becoming linked to North America in the north. Africa was isolated, except to the north, where, with the drying up of the Tethys Sea, it became joined to Europe and Asia in the Northern Continent. Farther east, India similarly became attached to Asia.

During the Miocene, Madagascar was separated from the African mainland, providing as in the case of New Zealand, a relict flora of great phytogeographical interest.

In the final epoch, the Quaternary, the polar regions appear to have come to lie in much their present positions, assuming with Koppen and Wegener that they had previously been disturbed. Together with the effect of the Pleistocene Ice Age, this readjustment had a profound effect on flowering plant evolution and distribution. The 'Malayan Flora' disappeared from Europe and Asia Minor, to be replaced by a temperate flora originating farther north. Near the Northern Ice-cap, in North America, and in Europe, a new flora of Arctic plants arose, comparable in mode of origin with, but three epochs younger than the Antarctic flora.

In the Southern Hemisphere the only land mass directly

covered by the Pleistocene Ice-cap was Antarctica, but the land floras of that hemisphere did not entirely escape the effects of the Ice Age. In Australia and New Zealand most of the tropical forms which had survived from Cretaceous times were destroyed by the increased cold.

In the Northern Hemisphere, temperate forms which previously had a continuous distribution from North America to Asia via the land bridge across the Behring Strait, would be driven southwards on either side towards California and China respectively.

When the Pleistocene Ice Age finally came to an end, possibly little more than 10,000 years ago, and milder conditions returned, the final separation of the continents had, according to Wegener, reached approximately the present position. The Arctic flora migrated northwards from Europe and North America, leaving Arctic-Alpine relicts on the high mountains. The 'Malayan flora' spread over the tropical parts of South-east Asia and Melanesia. Australia and New Zealand evolved many endemic forms from their relict Cretaceous floras; Madagascar did likewise from its Miocene flora. In Southern Africa, where the primary differentiation of Herbaceae and their major branch the Monocotyledons had taken place, and the early differentiation of the Lignosae had proceeded, a very great range of flowering plant groups survived, providing a far greater family representation than any other comparable area of the world.

While much speciation must have occurred in the Tertiary and Quaternary epochs, this took place largely within the family distribution determined by the final break-up of the two ancient continents in the Cretaceous. If this hypothetical account of flowering plants is true, on the average only one new family would appear approximately

every million years. It is not then surprising if little major evolution in the flowering plants has taken place within the 10,000 years or so which have elapsed since the last Ice Age, nor that many modern minor taxa appear to be from their morphology, cytology, and distribution quite ancient groups.

This hypothesis here presented of the origin of flowering plants has been developed primarily from a study of distribution phenomena in modern plants. It is by no means basically a new contention, as will appear later from a discussion of the works of Camp, Croizat, and others. What is original is the relationship of the 'Southern Origin' hypothesis to the theory of Continental Drift, and the outline of the time and place of flowering plant evolution, with the special reference to the African continent.

The hypothesis might clearly be either substantiated or disproved by palaeontological means, were fossil deposits richer and more easily explored, and fossil evidence of a negative as well as a positive character. The bearing of existing fossil evidence on the hypothesis can be briefly reviewed.

FOSSIL DISTRIBUTION

The most relevant existing fossil records are to be found in Cretaceous deposits of the Northern Hemisphere. These are usually interpreted as indicating basically two types of flowering plant floras, a tropical and a temperate.

The tropical Cretaceous flora, previously referred to here as the 'Malayan flora', appears to have had its northern and southern limits approximately in the London Basin and the Egyptian Delta respectively (Reid and Chandler, 1933; Chandler, 1954). This flora is characterized by the presence of members of tropical families in the section Lignosae of

only moderate taxonomic advancement, such as Lauraceae, Myrtaceae, and Anacardiaceae, with a form of the palm genus *Nipa*. A number of authorities consider with Kryshtofovich (1929) that a portion of this 'Malayan flora' has remained in the tropics of South-east Asia 'unmolested ever since its first descent from its Cretaceous ancestors'. Reid and Chandler (1933) likewise, and contrary to Seward (1934), believed that the 'Malayan flora' of the London Clay had arrived there by migration north and west along the shores of the Tethys Ocean from South-east Asia to Western Europe. There are also sufficient fossil records to suggest (Seward, 1934) that this 'Malayan flora' continued westwards beyond Europe and across what is now the more southerly part of the U.S.A.

To the north of this tropical belt of Cretaceous 'Malayan flora' there are many fossil remains of a temperate flora. This is particularly well represented in Greenland, where Cretaceous fossils have been referred to early temperate families of the Lignosae like Magnoliaceae, Juglandaceae, and Fagaceae, and to early temperate Herbaceae such as Ranunculaceae and Rosaceae. This temperate flora is represented in Cretaceous fossils from many other of the modern north temperate countries, often occurring mixed with elements of the tropical flora. It is also encountered in the Southern Hemisphere, again mixed with more tropical elements. For example, from the New Zealand Cretaceous Stopes cites records of three species of *Quercus*, and two of *Ulmophyllum*, with a species of *Sapindophyllum* and of *Palaeocassia*; from Australia, six species of *Quercus* with one of *Proteoides*.

In the succeeding Tertiary epoch flowering plant fossils become especially abundant, and more readily referable to modern genera and families. The composition and

distribution of Tertiary floras is comparatively well known, especially in the Northern Hemisphere.

This is how one palaeontologist describes adjustments during the Tertiary epoch to the Cretaceous distribution of flowering plants (Chandler, 1954):

> . . . when during the Oligocene the connection of the Tethys with the Indian Ocean was broken, so that the former vast waterway became a huge land-locked Mediterranean, while the great transcontinental mountain barriers of Eurasia were being uplifted, progressive cooling of the climate in middle latitudes occurred, so that more temperate plants from the North gradually supplanted the former tropical ones of the Eocene. . . . In Africa the course of events may have been somewhat similar . . . the Tethyan flora must have been driven from the more northerly part of its former Cretaceous and Eocene territory by the pressure of unfavourable conditions. But it could probably have survived in the tropics of Central Africa. Dessication combined with the southern trend of plant migration in post-Oligocene times would undoubtedly have prevented any later return to the more northerly latitudes it had previously occupied. Deserts and the Tethyan sea (or its shrunken remains) would probably have cut it off effectively from Asia. But within the African equatorial belt it may have persisted, possibly giving rise (or giving place?) eventually to a distinctive African tropical vegetation as it evolved in isolation from the Asiatic stream of life.

Chaney (1940, 1947) showed that there was a gradual displacement of temperate to warm-temperate Cretaceous forests in low and middle latitudes in the United States at the end of the Cretaceous, their being replaced by warm-temperate to sub-tropical vegetation derived from the Antillean region on the east and Mexico and Central America on the west. Since the Oligocene these warm and sub-tropical elements, Chaney points out, have been

gradually moving south again, giving way to a temperate Tertiary flora.

Of this temperate Tertiary flora Seward (1931) says,

> In the earlier part of the Tertiary period the Tethys Sea continued to form a barrier between Europe and Africa; in the Miocene stage began the great upheaval which culminated in the Pliocene stage, and a barrier of mountain ranges, stretching from the Alps to the eastern limit of the Himalayas, was thrown across Europe and Asia. . . . In the Cromerian flora only 5 per-cent of exotic or extinct species are recorded and the Chinese–North American element has almost disappeared. It is therefore abundantly clear that the forests which had long been established across the northern hemisphere in the earlier part of the Pliocene stage were composed of an overwhelming number of plants which to-day are either extinct or for the most part still living in the Far East or in North America, but not in Europe. . . .

Such fossil evidence as exists, which it is possible to mention only in outline, is therefore not incompatible with the hypothesis of flowering-plant origins presented. No really conclusive evidence is available bearing either way, but this might be obtained by critical examination of the microfossils of Cretaceous, Jurassic, and earlier rocks. Before the Cretaceous, flowering plants may have formed such a small percentage of individuals in the total world vegetation that the chances of their definite identification other than from microfossils are not great.

Mention must be made here of a recent discovery in Southern Africa which has considerably excited palaeontologists. Plumstead (1952) has described two new genera and six new species of fructifications borne on *Glossopteris* leaves, the first occasion on which the fruiting material has been demonstrated in connexion with the leaves.

Concerning the phylogenetic significance of these discoveries the author states: '. . . the growth of the small sacs in *Lanceolotus lerouxides* directly on a cushioned and modified surface of the leaf, and the development of a separate bract-like protective cover for them, seems to the author to be an earlier stage in development from ferns to flowering plants than any shown in other pteridosperms'.

MODERN DISTRIBUTION PHENOMENA

In the absence of conclusive fossil evidence bearing on the hypothesis here presented it is necessary to seek confirmation by further examination of distribution phenomena among modern flowering plants. The evidence of flowering plant migration provided from distribution phenomena falls into two main categories. Firstly there are the relict floras, island floras such as those of New Zealand and Madagascar, or specialized floras such as the 'Cape flora' and the Arctic flora. Secondly, there is evidence accruing from an examination of the total distribution of particular taxa.

THE CAPE FLORA

The 'Cape flora' in South Africa is almost entirely restricted to the Cape Peninsula and adjoining isolated mountain masses. It is characterized more especially by the presence of plants in the families Proteaceae, Restionaceae, and the endemic Bruniaceae, and of numerous representatives of the Papilionaceae, Polygalaceae, Compositae, and Rutaceae. Excepting Bruniaceae and Restionaceae, these families are fairly well represented by other forms farther north in Southern or even Tropical Africa; all are considered to represent an approximately intermediate position in flowering plant evolution. Weimarck (1941) states,

'The abundance of species within the Cape and especially the occurrence of a large number of endemic systematically isolated genera leads to the view that the Cape Flora represents a very old element in the plant world.'

It has been suggested earlier in this account that the 'Cape flora' evolved from an ancient temperate flora as an Antarctic flora during the Cretaceous when plants were exposed to cool conditions near the comparatively small South Polar Ice-cap. Under these conditions specialized forms of already established families such as Papilionaceae, Polygalaceae, Compositae, and Rutaceae could be formed, and quite new families could evolve from the ancient representatives of other already widespread family groups like Restionaceae from Juncaceae, Proteaceae from Thymeliaceae and Bruniaceae from Hammamelidaceae. This suggestion is not incompatible with the theory of a 'northern' origin of the 'Cape flora' put forward by Levyns (1938, 1952) after detailed studies of the distribution of certain 'Cape' genera.

A general consideration of the characteristics of the 'Cape flora' obviously requires separate treatment. The salient features of importance are that this predominantly shrubby and herbaceous vegetation contains approximately equal representation of families in Herbaceae and Lignosae, and that Monocotyledons are well represented (Adamson and Salter, 1951). The species representation is rather greater in the Herbaceae, but in all groups there are comparatively few species as compared with genera. The ratio of Monocotyledons to Dicotyledons in the 'Cape flora', according to the above authors, is 1:2·02, rather less than elsewhere in the world where the ratio, according to Good (1951), is usually 1:2·5–4. This low ratio in the Cape might indicate an environment especially favourable to

Monocotyledons, or else confirm the supposition of their origin from Herbaceae somewhat in that region. Apart from families endemic in this 'Cape flora' very few families are represented which do not also occur in the modern vegetation of tropical Africa. The generic representation, on the other hand, is not nearly so close.

All these special features of the 'Cape flora' strongly support the theory postulated here as to its origin. The survival of this 'Cape flora' in the Cape area of South Africa has not yet been fully explained, but it must be associated with the long occurrence there of high relief, that is mountains even now still reaching 7,000 ft. high, and a winter rainfall.

Wegener's modified theory postulates that during the Cretaceous the southern extremities of Africa and South America were still joined to one another, and that both were linked through Antarctica to Australasia (Fig. 3). The 'Cape flora' would evolve and spread round the South Pole over all these areas. On that part of Gondwanaland which is now Africa, it may at one time have extended northwards to the boundaries of Central Africa, for remnants of it still survive in Madagascar and the Rhodesias (Weimarck, 1941; Wild, 1956). In South America and Australia fewer representatives of the flora persist today, but there are sufficient to provide evidence in support of the general hypothesis here presented.

THE ARCTIC FLORA

Although also arising from contact between an existing flora and the cold conditions near a fluctuating ice-cap, the Arctic flora is more recent than the 'Cape flora'. During the Cretaceous and Tertiary epochs, on the Koppen-Wegener hypothesis, warm conditions prevailed over the

lands now lying within the Arctic Circle. The small North Polar Ice-cap of these times was formed largely over the sea, too distant greatly to influence any land flora.

The Arctic flora would evolve when the Pleistocene North Polar ice, forming in approximately the present North Polar position, approached the temperate flora of the disintegrated ancient Northern Continent of Laurasia. The tropical flora of Laurasia had already been driven south by the readjustment during the close of the Tertiary epoch of the earth's polar centres and the location of the Equator about where it lies today. The distribution of temperate families in Europe and North America, which separated during the Late Cretaceous, would be much as it is today, and two distinct Arctic floras would form by a largely random evolutionary selection in these two separate areas.

As regards the actual mode of origin of the Arctic flora, it is now generally believed (Stebbins, 1947) that hybridization and chromosome doubling occurred in northern species populations which came together after long periods of isolation in glacial refugia. Because of the selection of favourable gene combinations among these new forms, the Arctic–Alpine flora contains a high proportion of polyploids. The two ancient Arctic floras have now been merged by the northward retreat of the ice, but it is considered, from independent evidence, that the modern Arctic flora has had two distinct origins. Further phytogeographical studies of the relict Arctic floras remaining in the Alpine vegetation of North America and Europe respectively, may also confirm the separate origins of these eastern and western Arctic elements. For present purposes it is sufficient to note the similarity of the origins of the Arctic–Alpine flora of the Northern Hemisphere and the

'Cape flora' of the Southern Hemisphere, separated as they are in time and space.

NEW ZEALAND

The flora of New Zealand is remarkable for its very high percentage of endemics, and it has other peculiarities. Although in a temperate region, New Zealand has by no means a *north* temperate type of flora. Herbaceae are well represented, with the notable exception of Monocotyledons. The entire monocotyledonous group derived from the Ranunculoideae by Hutchinson is absent, apart from the Zosteraceae, which have a marine distribution. Grasses are not prominent, and one genus of the 'Cape flora' Restionaceae has survived. Lignosae are poorly represented, and such families as are present are either primitive, like the Magnoliaceae and Rosaceae, or not especially advanced and largely tropical families like Pittosporaceae, Sapotaceae, Lauraceae, and Monimiaceae.

Taken in conjunction with the presence of the tropical monocotyledonous families Palmae and Pandanaceae, this would suggest that New Zealand became isolated in a warm period before the more advanced groups of the Lignosae and Monocotyledons had had sufficient time to migrate to it, although elements of the Antarctic 'Cape flora' had reached it in the form of Restionaceae, Proteaceae, and Cunoniaceae. New Zealand is considered, as mentioned earlier, to have been isolated during the Cretaceous. On the hypothesis submitted here, New Zealand was the territory of Gondwanaland most distant from the centres of evolution of the early Herbaceae and Lignosae. Slow migration, perhaps coupled with unsuitable habitats, may well have retarded until too late the migration of the more advanced forms to this distant land.

Further evidence could be considered from island floras such as those of Madagascar and the islands in the Gulf of Guinea or from that unique and interesting island New Caledonia, but space must be left for the mention of other points regarding the second line of support in the form of distribution relationships.

SOUTH POLAR DISTRIBUTION

The distribution of flowering plants from a focal area in the Southern Hemisphere has been demonstrated with an imposing mass of evidence by Croizat (1952). Unfortunately his work has not, perhaps sometimes for personal reasons, always received due consideration. Too often criticism has been made of his general thesis by reference to relatively unimportant details which are not an essential part of his principal argument.

Croizat's main contention is that all flowering plant groups can be shown to have originated in one particular area of the Southern Hemisphere, and to have migrated thence via three main routes. As the groups migrated they differentiated, throwing off taxa of varying importance, whose interrelationships can now be used to trace the original migration route. He deliberately avoids attempting to relate these migration routes to past or present land distribution, and perhaps thereby loses some support for his theory, although to ignore past land distribution is quite logical, and indeed as already mentioned is strongly advocated by Jeffreys (1951).

Justice cannot be done to Croizat's work without lengthy consideration, but perhaps one example selected from the many he cites may illustrate how in general it is not in conflict with the present hypothesis of the origin of the flowering plants. In Fig. 10 of his book Croizat illustrates

the route of migration of *Evolvulus*, section Alsinodei, subsection Pedunculati. The family to which this group belongs is Convolvulaceae, a cosmopolitan family, fairly advanced,

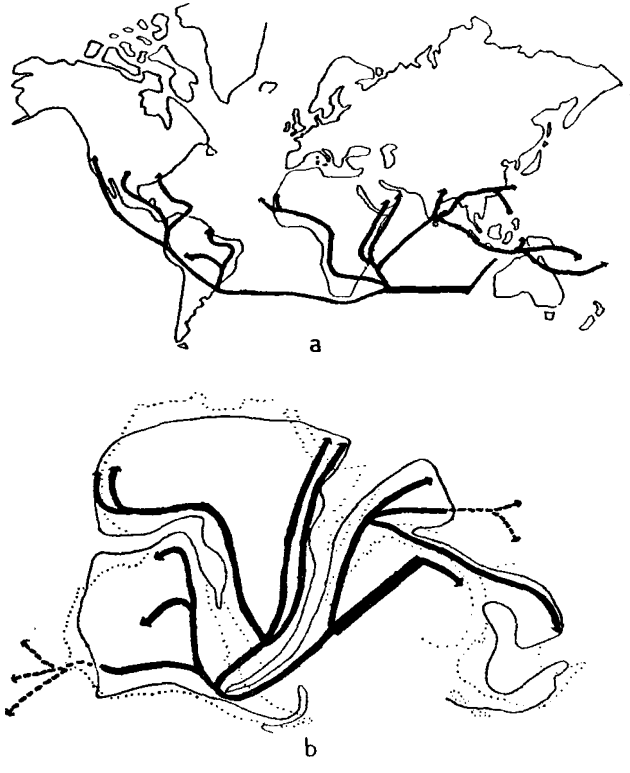

FIG. 4. Distribution of *Evolvulus*, section Alsinodei, subsection Pedunculati (*a*) after Croizat, (*b*) during Early Cretaceous on Wegener's continental reconstruction

but well differentiated by the Cretaceous as witnessed by its occurrence in New Zealand. *Evolvulus*, one of the more primitive groups in the family, must have evolved as a tropical genus by Early Cretaceous times and have spread over the warmer part of Gondwanaland (Fig. 4). Various sections of the group would be isolated in the Late Creta-

ceous with the break-up of Gondwanaland, but the Tertiary junction of the two American continents would permit the South American section to spread up into Central and North America. The Indian section, likewise affected by India's junction with Asia, spread eastwards into Asia and the Malay peninsula. The Australian section would have been distributed over the Polynesian Islands before the break-up of Australasia. If the cyto-taxonomy and genetics of the Pedunculati section of *Evolvulus* could be worked out, independent evidence for or against these suppositions might be obtained.

Croizat makes one reference to the antiquity of Angiosperms which is very interesting as an independent suggestion paralleling what has been considered here. He says,

> We find in Cretaceous beds of Alaska and Greenland fossils of *Platanus*, *Acer*, &c., which we have no difficulty in identifying, for they resemble their living descendants in every essential. The species may themselves no longer exist, but the genera are modern. This means that *Platanus* and *Acer* endured for something like 80,000,000 or 120,000,000 years to this day, which prompts us next to inquire, how long did it take these genera to become modern out of the primaeval angiospermous matrix? The question is speculative, of course, and so must be the answer. It is within sober reason, however, that *Platanus* and *Acer* began to differentiate long aeons of geological time before the Cretaceous, and the most conservative estimate is bound to place their ultimate origin in the Permian, indeed, most likely in the Carboniferous.

Leaving Croizat, cyto-taxonomy, and genetics for a moment, an attempt may be made to simplify distribution phenomena and classify these by their epoch-dating. Fig. 5 illustrates the land distribution according to the modified Wegenerian hypothesis at three selected periods of

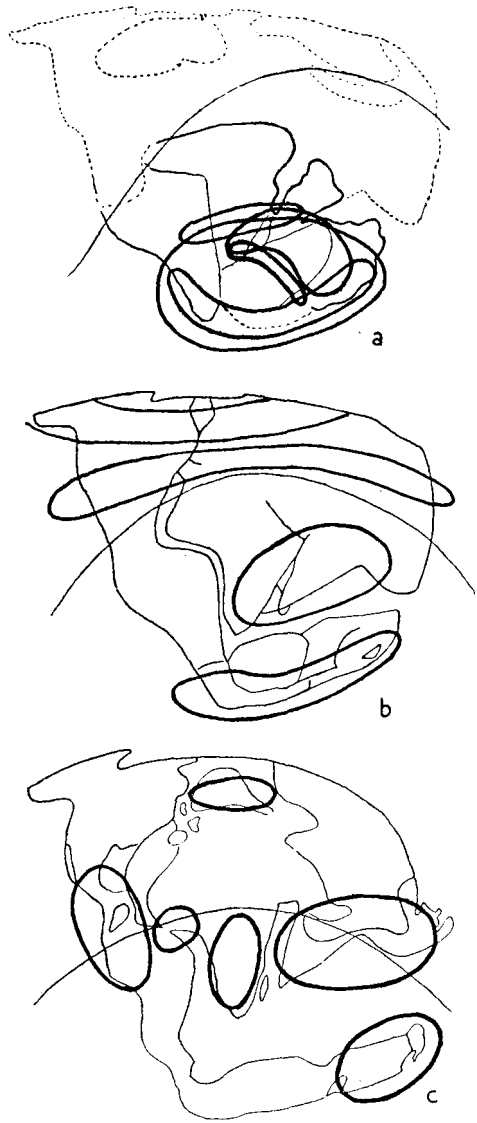

FIG. 5. Land distribution during the (*a*) Jurassic, (*b*) Cretaceous, and (*c*) Eocene periods according to Wegener and du Toit, together with the principal expected family and larger generic distribution

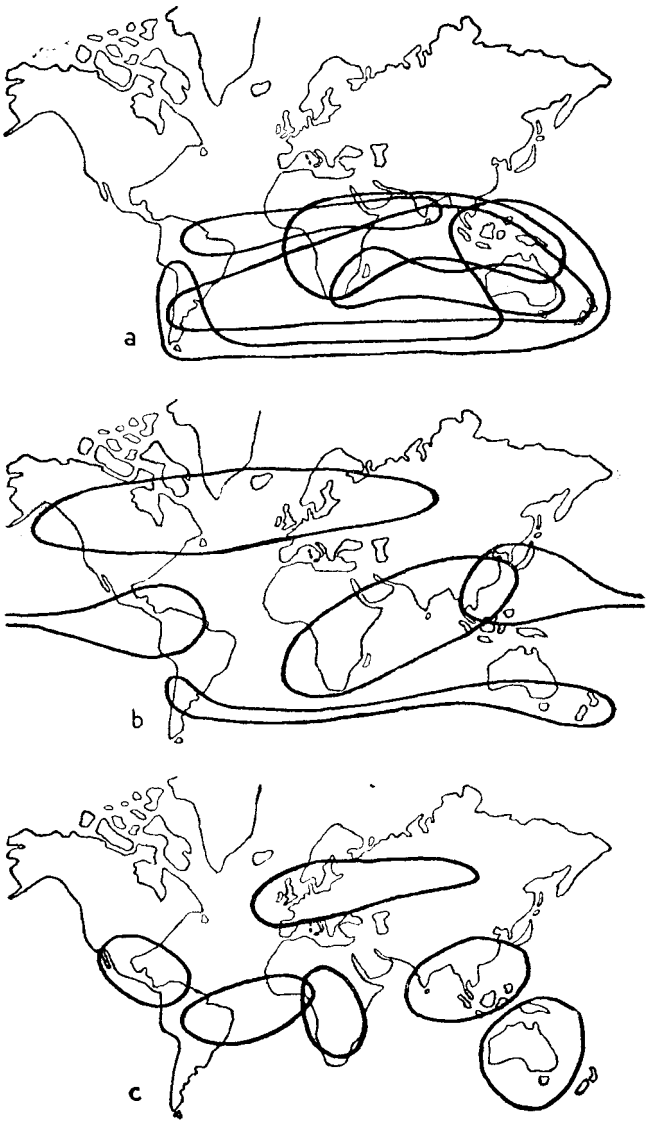

FIG. 6. Projection of the (*a*) Jurassic, (*b*) Cretaceous, and (*c*) Eocene distribution phenomena illustrated in Fig. 5 on to the modern continents

theoretical flowering plant development. The expected main types of distribution during each of these three periods is indicated, and in Fig. 6 these are translated into the modern continental distributions.

Most distribution phenomena chosen from the examples provided from the works of authors interested in phytogeography (Hutchinson, 1946; Wulf, 1950; Croizat, 1951; Good, 1953) and from other sources, may be fitted into this simplified scheme of distributions. A consideration of the illustrations cited by these authors shows the implication that, for example, Velloziaccae, Mayacaceae, and Ruscaceae are much more recent groups than Restionaceae, Monimiaceae, and Philesiaceae. According to both the subjective judgement of Hutchinson (1926, 1934) and the statistical assessment of Sporne (1949) they are so related in time. It must, however, be borne in mind that sometimes distribution phenomena are permitted to weigh heavily in systematic considerations, also that geological periods were continuous and any classification into Jurassic, Cretaceous, and so forth distributions must always be an arbitrary division.

A brief but very important exposition of the southern origin of flowering plants by Camp (1947) actually preceded the comprehensive work of Croizat. Camp similarly discusses modern discontinuous distribution phenomena in relation to past dispersal and group origins, without reference to previous land distribution. Most significantly he for the first time introduces cyto-taxonomical evidence in support of his deductions.

Camp's conclusions as to the time and place of flowering plant origins are substantially similar to those submitted here. He states,

Pressed for a place and date, I would say that it seems likely that the angiosperms, as a group, arose on this southern land

mass contemporaneously with the Paleozoic of the northern (Holarctic) land mass and that the divergence of the basic, generalized familial groups had been accomplished on this southern land mass certainly by the mid-Mesozoic. The great bulk of the angiospermous families (at least their woody members) and many of their present-day genera, appear to have been evolved by the Cretaceous.

On such tests as can at the moment be applied, which exclude detailed and comprehensive cyto-taxonomic investigations, it therefore appears that the foregoing general hypothesis regarding the origin and mode of distribution of the flowering plants is not in conflict with evidence from a number of relevant fields.

EVOLUTION OF MODERN AFRICAN FLORAS

With this general hypothesis as to the mode of origin of flowering plants in mind, it is now possible to proceed to offer an explanation for the origin of the basic sections into which the African flora was earlier in this address divided.

From their Permo-Carboniferous beginnings, temperate elements of the Herbaceae were, during the Triassic and Jurassic periods, differentiating in the cooler areas of that part of Gondwanaland which later became Southern Africa. These Herbaceae were associated with the first temperate groups of Lignosae, and formed the original floral unit from which the temperate flora of what is now South Africa and the mountain flora of Tropical Africa were derived. Farther to the north-east in Gondwanaland many elements of this floral unit migrated across the Tethys Sea into the Northern Hemisphere, giving rise to the modern north temperate flora. Differentiation had proceeded sufficiently in these migratory elements during the Permian for the emergence of such genera as *Cardamine*, *Nasturtium*,

Stellaria, *Viola*, and *Vaccinium*, whose present distribution includes such widely separated areas as Britain, Madagascar, and South America. As was also discussed earlier, the parent temperate flora, where it was exposed to extreme cold, had by Early Cretaceous times evolved the Antarctic 'Cape flora'; the area occupied by this new flora would include part of what is now Southern Africa.

Increasingly warm conditions during the Triassic and Jurassic epochs permitted the development by the Early Cretaceous of a band of tropical vegetation in Africa between the ancient temperate flora and the deserts then covering what is now Equatorial and North Africa. This tropical vegetation was principally derived from the tropical woody groups of the Lignosae, but it also contained certain newly evolved tropical elements of the main branch of Herbaceae and its off-shoot the Monocotyledons. This second and tropical flora extended beyond Africa, westwards to modern South America, eastwards along the coast of what is now India, and north across the Tethys Sea into the Northern Hemisphere, as the 'Malayan flora'.

The ancient Permian, Triassic, and Jurassic temperate flora of Africa contained both woody and herbaceous plants, which probably by the Cretaceous would under favourable conditions associate to form a rather open woodland type of vegetation. During the Tertiary this flora was in places exposed to very arid conditions, and in such areas it developed savanna or steppe types of vegetation, with plant forms of an increasingly xeromorphic character. These xerophytic floras survive today as the vegetation cover of much of the low and high veld of South Africa, mixed to a greater or lesser extent with similar but intrusive elements from the tropical vegetation to the north. The great range of families represented in

these temperate or sub-tropical veld floras of South Africa today bears witness to their origin.

Other portions of the ancient temperate flora were finally isolated by various orogenies and climatic changes on a number of scattered high African mountains (Fig. 1). Because this mountain flora was not in general exposed to arid conditions, it largely remained taxonomically and morphologically close to the ancient temperate African flora.

On the mountains at medium altitudes, where precipitation was adequate and soil cover sufficient, closed forest was established. Higher on the mountains, where conditions were more extreme with less water and soil, a more open type of vegetation continued. It is possible that some very early forms of plant development, long since extinct elsewhere, have survived as relicts here. These are best illustrated by the giant *Lobelias* and *Senecios* of the East African mountains. As Skottsberg (1928) has described, the 'tree' Lobelia species still survive besides at high altitudes in India, Ceylon, and the Philippines, with allied forms in Hawaii and Brazil. The latter also occur in the mountains of the Federation and of West Africa. Such a pantropical montane distribution could be expected only for a widespread element of this temperate Permian to Cretaceous flora, and without the present hypothesis a discontinuous distribution such as is shown by these modern 'tree' Lobelia species is impossible to explain.

In some highland areas of Africa like the Jos Plateau or the Fouta Jallon Massif, conditions were unsuitable for the establishment or survival of the forest element, and only the more arid and predominantly grassland type has persisted.

The Cretaceous tropical woody 'Malayan flora' during

the Tertiary continued to evolve into the modern Tropical Rain Forest. The African section was separated by Early Cretaceous times from its counterparts in the Northern Hemisphere, India, and South America, although later temporarily rejoined to the latter. The comparative floristic paucity of the modern African Rain Forest as compared with its South American and more particularly its South-east Asian counterpart has frequently been remarked. It is possible that during the Tertiary and Quaternary periods Africa was subjected to vicissitudes of climate not experienced in the other continents. There is some evidence at least that Africa alone was subjected, as regards its equatorial regions, to several drier periods contemporaneously with the Pleistocene Ice Age.

During the Tertiary this woody forest flora in Africa was exposed towards the north to the arid conditions of an extensive desert. Here would develop from it the numerous vicariant forms of the modern Lowland Savanna. At its southern and eastern margins this ancient lowland forest colonized higher ground and came into contact with the mountain forest of the temperate floral unit. When also exposed to arid conditions, vicariant savanna genera and species were similarly evolved from these high colonists. Some savanna elements with a wide climatic and edaphic tolerance such as the genera *Acacia* and *Grewia* spread through both the northern Lowland and southern and eastern Upland Savanna. Others, less tolerant, or perhaps more recent, such as *Brachystegia* in the south or *Anogeissus* in the north, still remain restricted to the one or the other.

This derivation of the African savanna elements from the ancient forest floras is supported by an analysis of family and generic representation. According to some

workers such as Duvigneaud (1952) the process has continued into recent times. Some indication of the period during which these African savanna elements were evolving may be deduced from their modern distribution. Aubréville (1949) cites a number of savanna species common to Africa and South America, and in certain cases Madagascar also. Where these are unknown from the Indo-Malayan region, an origin during the late Cretaceous or early Tertiary (Miocene) periods is implied. Certainly the Lowland and Upland Savanna floras of Africa are younger than the Lowland Rain Forest flora, which in its turn post-dates the Mountain Forest and Mountain Communities and their junior relative the 'Cape flora'.

During the Quaternary there occurred the final major changes in the areas occupied by these basic African floras. The Quaternary orogenies isolated eastern fragments of the Lowland Tropical Forest flora from the main mass in the west, and virtually isolated the two savanna floras to the north and south of this forest, previously linked on the eastern side of Africa.

This account of the origin of the components of the African flora finds some confirmation in the distribution and composition of certain elements in their constitution.

The South African temperate flora is now mainly a specialized steppe and savanna flora, but the distribution of its genera reveals its origin from the widespread and partly differentiated temperate Herbaceae, together with the earlier temperate groups of Lignosae. The Table shows a list of the basic genera and families of New Zealand common to South Africa, Britain, and the largest area in West Tropical Africa where a direct derivative of the Permian to Cretaceous African temperate flora survives, the Cameroons Mountain. Although all four floras have

diverged very considerably as regards speciation since the Cretaceous, their close taxonomic relationship at the generic and family level is very clear.

TABLE

Families and Genera occurring in New Zealand, Britain, South Africa, and over 4,500 ft. on the Cameroons Mountain

Urticaceae
Loranthaceae
Santalaceae
Polygonaceae
Rumex
Carophyllaceae
Stellaria
Hypericaceae
Hypericum
Ranunculaceae
Clematis
Cruciferae
Rosaceae
Rubus
Papilionaceae
Geraniaceae
Geranium
Apocynaceae
Verbenaceae
Labiatae
Scrophulariaceae
Veronica
Rubiaceae
Campanulaceae
Wahlenbergia
Lobelia
Linaceae
Plantaginaceae
Plantago
Euphorbiaceae
Euphorbia
Malvaceae
Violaceae
Viola
Thymelaceae
Arialaceae
Umbelliferae
Hydrocotyle
Ericaceae
Primulaceae
Oleaceae
Gentianaceae
Boraginaceae
Myosotis
Solanaceae
Solanum
Lentibulariaceae
Utricularia
Cucurbitaceae
Compositae
Senecio

There are indeed a number of *species* of this ancient temperate flora with a present distribution extending from Britain across Europe and the high mountains of Africa to South Africa, like *Aira caryophylla*, or reaching as far south as Southern Rhodesia, for example *Sibthorpia europaea* (Hedberg, 1954). Other high-altitude species such as *Desmodium repandum* spread over the mountains of Africa and of the islands of the Indian Ocean, reflecting what can be called a montane 'Gondwanaland' distribution, or as in the case of *Viola abyssinica* and *Cardamine africana* are discontinuously pan-African and also occur in Madagascar.

The most remarkable distribution is that shown by *Gnaphalium luteo-album*, which reaches from the Channel Islands to New Zealand, although this species might possibly be an introduction in some areas. Because trans-Tethys migration is considered here to have been possible only during the Permian and Triassic periods, such species must be very old, unless either a polytopic origin is postulated for them, or they are regarded as examples of fortuitous long-distance dispersal.

The great antiquity of certain polyploid species has recently been demonstrated (Stebbins, 1947). Two species of *Oryzopsis* are thought to have originated in the Miocene, while it is possible that a group of tetraploid New World species of *Gossypium* could date back to the Cretaceous. If an age of over 100 million years is thus considered possible, a date of 150 million years ago for the origin of a few species such as the two first mentioned in the above paragraph is not inconceivable.

Time permits only scanty reference to the derivation of the Upland and Lowland Savanna from the parent flora which has now, in modern form, occupied the Tropical Rain Forest. A comparison of the family representation reveals that a considerable number of forest families, such as the Celastraceae, Begoniaceae, Rapataceae, Erythroxylaceae, Lauraceae, and Monimiaceae, have apparently not evolved a significant number of savanna forms. Inability to evolve reproductive isolating mechanisms might have prevented certain forest families from developing savanna species. On the other hand there are very few savanna families which, like Capparidaceae, Tamaricaceae, and Pedaliaceae, have no forest section. Taxonomically the savanna floras are a smaller derivative of the systematically wider forest flora. At the same time the multiplicity of

forms frequently encountered in predominantly savanna genera is indicative of a secondary stage of evolution.

Stebbins (1947) points out that rapid evolution requires the presence of a rapidly changing secular environment, but that not all plant groups exposed to such changes can respond to them. As Stebbins also remarks, in habitats which remain constant for long periods of time, most of the plant groups tend to evolve increasingly slowly. The African forest flora, like the African mountain flora, has accordingly become more and more stabilized. Recent plant evolution in Africa has taken place largely in the savanna elements; latterly it has proceeded especially in those savanna taxa, native or introduced, which have been able to invade the vast man-made clearings in the natural vegetation, and to survive the universal annual grass fires which man has greatly promoted, if not actually introduced into the African scene.

It is not possible to go further into the relationships of these different floras at this time, but evidence sooner or later will be provided, probably by biogeographical work based on cyto-taxonomical and genetical researches, as to the validity of this explanation of the origin of the several African floras, and their place in the world's past and present vegetation. Fossil evidence also could provide relevant information, but it is, generally speaking, so scattered, and unless new techniques for dealing with microfossils are evolved, so difficult to obtain, that it seems unlikely, with the important exception mentioned in this address, to be of much assistance in the immediate future. The onus of proof remains for the moment, as in certain other major fields of research, with the cyto-geneticist.

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